Lycianthes starbuckii and Lycianthes rzedowskii (Solanaceae), Two New Species of Perennial Herbs from Mexico

Ellen A. Dean

University Herbarium, University of California at Berkeley, Berkeley, California 94720, U.S.A.

ABSTRACT. Two new species of Lycianthes series Meizonodontae from Mexico are described and illustrated: L. starbuckii E. Dean and L. rzedowskii E. Dean.

Lycianthes comprises about 200 species (D'Arcy, 1991) with a distribution that encompasses Mexico, Central America, South America, and some regions of Asia and the Pacific. The genus was last monographed by the German botanist Georg Bitter (Bitter, 1919), and although his work remains the most complete reference for Lycianthes, its impenetrability has probably discouraged more students than it has inspired. Thus, the best recent publications on the genus are floristic treatments (see D'Arcy, 1973; Nee, 1986; Gentry & Standley, 1974; Barboza & Hunziker, 1992). Workers who have completed floristic treatments of the genus have commented on the paucity of herbarium collections of some Lycianthes species and have suggested that this might be due either to the relative rarity of some of the species (D'Arcy, 1973) or the nocturnal flowers many of them possess (Nee, 1981).

Most Lycianthes species are trees, shrubs, or vines; less than ten percent are perennial herbs. Bitter's Lycianthes series Meizonodontae is one group of perennial herbs, distinguished by their combination of large tuberous storage roots, single-flowered inflorescences, large fruits, and large dark seeds. As part of a taxonomic revision of the series, it has become necessary to describe two new species.

TERMINOLOGY

As with all Lycianthes and many species of tribe Solanae, the branching pattern of the species of series Meizonodontae combines early monopodial and later sympodial growth. The aboveground stems emerge annually during the summer rainy season and die back during the winter dry season. The first stem-segment to emerge from the root is monopodial, with the leaves spirally arranged, usually terminating in an inflorescence or bud; thereafter, the branching pattern is sympodial, with each stem-unit difoliate, the leaves usually geminate, each unit end-

ing in either a flower or bud (Child & Lester, 1991). Lateral branches growing from leaf axils of the first monopodial stem repeat this pattern of early monopodial and subsequent sympodial growth.

The flowers of all of the species of series Meizonodontae are oriented plagiotropically (laterally) due to a slight curvature at the tips of the pedicels. For three to five days in a row, the flowers open each morning, closing after several hours. The rotate corolla, which enlarges each day that it opens, is divided into five fleshy lanceolate segments that are connected nearly to their tips by thin translucent corolla tissue. I will use the terms corolla lobes and corolla membrane to refer to the segments and translucent tissue, respectively. As the corolla enlarges, the stamen filaments elongate, resulting in asynchronous anther dehiscence. Often two dehisce the first day, two the second day, and the fifth on the third day.

Lycianthes starbuckii E. Dean, sp. nov. TYPE: Mexico. México: Sierra de Nanchititla, oak forest across the reservoir from the town of Nanchititla, 1,945 m, 8 Nov. 1991, E. Dean et al. 315 (holotype, UC; isotypes, BM, ENCB, MEXU, MO, NY, XAL). Figure 1A-G.

Herbae perennes ramosissimae prostratae vel ascendentes. Folia sympodialia crasse chartacea, basi cuneata, apice acuta vel obtusa. Inflorescentiae uniflorae. Flos dentibus calycinis sub anthesi flexuosis, laxis, non reflexis; corolla lilacina rotata; filamentis staminalibus inaequalibus, duobus summis brevissimis, duobus lateralibus longitudine intermediis, infimo longissimo sed lateralibus semper minus quam 2-plo longiore. Fructus ovoidei atropurpurei granulis scleroticis carentes; seminibus nigris.

Perennial herbs from tuberous storage roots, to 15 cm tall, usually prostrate. Indument of simple, acute, several-celled trichomes, present throughout. Stems emerging from buds on the root crown; underground stems whitish, the leaves undeveloped; aboveground stems green-purple, prostrate to ascending, highly branched from near the soil level, terete in cross section; aboveground portion of monopodial stem segment usually very short, 0.5—



Figure 1. Lycianthes starbuckii E. Dean (A-G) and Lycianthes rzedowskii E. Dean (H-L). L. starbuckii (from E. Dean et al. 315): —A. Fruiting plant. —B. Enlargement of flowering sympodia illustrating floral bud development typical of series Meizonodontae. —C. Calyx at anthesis. —D. Gynoecium. —E. Enlargement of stigma (typical of L. rzedowskii as well). —F. Stamens (left to right: lowest, lateral, upper). —G. Mature fruit. L. rzedowskii (from E. Dean & T. Starbuck 212 and 322a): —H. Fruiting plant. —I. Calyx at anthesis. —J. Flower. —K. Stamens (left to right: lowest, lateral, upper). —L. Gynoecium. (Drawn by the author.)

3(-18.5) cm long; sympodial growth extensive, often forming mats, with both monochasial (one-sided) and dichasial (two-sided) branching points occurring in an unpredictable pattern, with dichasial fork angles 60-180°; sympodial units 2 mm long, 1 mm wide at tips of plant, 1.2-3 cm long when subtending newly opened flowers, the oldest sympodial units 0.7-5.5 cm long, 1.5-4 mm wide. Stem pubescence similar throughout, stems pilose to velutinous with trichomes 0.25-0.5 mm long near the soil level, these shorter distally 0.1-0.25 mm long. Leaves of first monopodial stem few, 2-5, spirally arranged, the first leaves often scalelike, the subsequent ones expanded, each larger than the one below it; ex-

panded leaves spathulate to obovate or oblanceolate, the margin entire, the tip broadly acute to rounded, cuneate at base and attenuate into petiole, this basal portion plus petiole accounting for \(^1/_3-^1/_2\) of total leaf length; mid-stem leaves to 3.3 cm long, 1.5 cm wide, the petiole to 0.8 cm long; the largest and distalmost leaf to 6 cm long, 3 cm wide, the petiole to 1.8 cm long. Sympodial leaves thick chartaceous, fleshier than those of other species of series Meizonodontae, the sympodial units difoliate, usually geminate, sometimes appearing unifoliate if subtending dichasial forks, or trifoliate due to bud expansion; largest leaves (often produced by first sympodial units) ovate to broadly elliptic to rhombic,

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the margin entire to undulate, the tip broadly acute to rounded, cuneate at base, becoming reduced, narrowed, elliptic, subsessile distally; geminate leaves similar in shape, unequal in size, the smaller $\frac{1}{4} - \frac{1}{2}$ the size of the larger, with more oblique leaf base, shorter petiole, and rounder tip, the largest leaves to 6 cm long, 3 cm wide, the petiole to 1.4 cm long (generally shorter). Leaf pubescence similar throughout, the leaves puberulent, the acute appressed trichomes adaxially 0.25-0.5 mm long, pointing uniformly toward the leaf margin, abaxially to 0.25 mm long, appressed-ascending along veins, the margins short-ciliate with ascending trichomes 0.25-0.5 mm long. Inflorescences one-flowered, terminating the stem-units, appearing to be opposite the geminate leaf-pairs or the single leaves of dichasial forks. Buds ovoid, the corolla at first included in the calyx and covered by the clasping teeth, then exserted, the corolla lobes pubescent abaxially, the calyx teeth lax. Pedicels at anthesis green with some purple, pilose with erect trichomes of two distinct lengths, the shorter (to 0.25 mm) regularly interspersed with the longer (0.5 mm); youngest buds (less than 5 mm long) subtended by short, erect pedicels, these elongating, becoming recurved then erect, 4.2-8.6 cm long when corollas open, usually surpassing the subtending leaves, curved only at tips, the flowers oriented plagiotropically. Calyx at anthesis green and purple, narrowly to broadly conical, 3-4 mm long, 4-5.5 mm wide, always broader than long, truncate, the margin with hyaline membrane, ten-ribbed, the ribs giving rise to 10 slender teeth that are 2-6.5 mm long, lax and flexuous, not reflexed, the ribs and teeth pilose, the spreading trichomes to 0.5 mm long. Corolla sympetalous; tube short, 1.5-2 mm, included in the calyx; limb rotate, 2.1-3.8 cm diam., with five valvate lobes connected nearly to their apices by the corolla membrane; lobes oblanceolate, lilac with 3-5 darker violet veins on adaxial sides, lilac and green on abaxial sides, curving backwards upon opening, slightly unequal in width, the upper 2.5-3.75 mm broad, the lower 3.25-5 mm broad, the tips curved inward in bud and remaining so as the corolla expands; membrane lilac, notched at the margin, with folds puckered outward on the adaxial side; pubescence of corollas concentrated on the abaxial side of the lobes, these puberulent with trichomes to 0.25 mm long, the lobe tips tufted with trichomes 0.1-0.3 mm long, the membrane sometimes short-ciliate near the lobes. Androecium of five stamens, the filaments of three different lengths, elongating each day the flower opens, the lowest stamen the longest, the two lateral of intermediate length, and the two upper the shortest; filaments pale green, glabrous, compressed lat-

erally, the filament of the lowest stamen 2.0-5.25 mm long, elongating more than the others (the lateral 1.5-3.75 mm long, the upper 1.25-3.25 mm), always less than twice the length of the lateral filaments; anthers dark yellow, exuding a sweet fragrance, lanceolate to elliptic, the lowest anther 3.25-4.75 mm long, the lateral anthers 3.25-5.0 mm long, the upper anthers 3.25-5.25 mm long, the pores of all anthers round and terminal. Gynoecium of two united carpels, the ovules 25-38; ovary conic to ovoid, 1.5-2.5 mm long; style straight to slightly curved, 7-10 mm long, the stigma capitate, shallowly lobed, slightly oblique, 0.5 mm diam. Fruit a berry without sclerotic granules, green when immature, at maturity glossy or dull dark purple-black, separating from calyx, 7-22 mm long, 7-17 mm wide, ovoid, the tip rounded to apiculate; fruiting calyx thicker and wider than at anthesis, 2-5.5 mm long, 6-12.5 mm wide, the teeth reflexed or spreading, sometimes breaking, drying as the fruit matures, 0.5-6.5 mm long; fruiting pedicel 5.2-12.2 cm long, deflexed, undulate (the attached fruit often lying on the ground), swollen at juncture to the calyx, the swelling 1.5-4.5 mm wide; seeds 2-29, rusty brown to black, reniform to suborbicular, 3.5-4.5 mm long, 3-3.5 mm wide, always longer than broad.

Distribution. Endemic to the Sierra de Nanchititla, in the southwestern part of the state of México, Mexico, on level oak forest floor, 1,945 m.

Lycianthes starbuckii flowers in July and August and produces fruits from October to November. It can be distinguished from other species of series Meizonodontae by its combination of prostrate to ascending (often mat-forming) habit, velutinous stems, thick blunt-tipped sympodial leaves with short cuneate bases, lax calyx teeth at anthesis, hairy corolla lobes, and dark purple fruits with large brown to black seeds. The only other prostrate species within the series are L. peduncularis (Schlechtendal) Bitter, a species restricted to dry eroded volcanic or limestone habitats, and L. moziniana (Dunal) Bitter, which grows along roadsides or in agricultural fields. Both have fruits that are green at maturity, and those of L. peduncularis have well-developed sclerotic granules. The habitat of L. starbuckii is distinct from those of closely related species. Although other species of series Meizonodontae grow in oak forest, they are generally found on moderate to steep slopes near drainages, while L. starbuckii is found on level forest floor.

This species is named for my husband and ace field assistant, Thomas Junn Starbuck, who has helped me in countless ways with my dissertation research. While walking near Nanchititla, he observed the

first plant of L. starbuckii after the rest of the group had stepped on it.

Paratype. MEXICO. México: District of Temascaltepec, Nanchititla, 18 Aug. 1933, Hinton et al. 4550 (BM, G, K, MEXU, MO).

Lycianthes rzedowskii E. Dean, sp. nov. TYPE: Mexico. Michoacán: Mpio. Charo, along hwy. 15, 20 rd. km E of Morelia, just E of Pontezuelas, 2,165 m, 13 Nov. 1991, E. Dean & T. Starbuck 322a (holotype, UC; isotypes, NY, XAL). Figure 1H–L.

Herbae perennes erectae vel reclinatae; caulibus monopodialibus (6-)10-21-foliatis. Folia membranacea vel chartacea, basi attenuata, apice acuminata. Inflorescentiae uniflorae. Flos dentibus calycinis sub anthesi erectis vel reflexis; corolla rotata alba venulis violaceis ornata; filamentis staminalibus inaequalibus, duobus summis brevissimis, duobus lateralibus longitudine intermediis, infimo longissimo sed lateralibus nunquam plus quam 2-plo longiore. Fructus elongati fusiformes vel conici, ad apicem attenuati, purpurati ad nigri, granulis scleroticis carentes; seminibus nigris.

Perennial herbs from tuberous storage roots, 1.7-11.0 dm tall, erect to reclinate (falling sideways with age). Indument of simple or branched, acute, several-celled trichomes present throughout. First monopodial stems one to several, first erect, then reclinate, emerging from buds on the root crown; underground parts of stems glabrous, white or purplish, the leaves undeveloped, often with stem-borne roots just below the soil level; aboveground parts of monopodial stems green to reddish purple, terete when fresh, collapsed, ribbed, when dry, 7-90 cm long, 2-8 mm at broadest point (at base or middle of stem); internodes 0.5-25 cm long, the shortest internodes near the base, the longest near the middle or upper part of the stem. Sympodial growth poorly developed compared with other species of series Meizonodontae, progressing laterally a total of 6-40 cm, shorter than initial monopodial stems; first two sympodial branching points usually dichasial (rarely only first branching point), appearing as forks, the fork angles often narrow, 60-90(-100)°, subsequent sympodial growth monochasial; sympodial units 0.5-5 mm long, 0.25-1.5 mm wide at tips of plant, (0.3-)0.8-2.7(-5.0) cm long, 1-2 mm wide when subtending newly opened flowers, the oldest sympodial units 1-11 cm long, 2-5 mm wide. Stem pubescence similar on monopodia and sympodia, young stems pilose to villous (sometimes glabrous), glabrate, trichomes 0.5-1.0 mm long, rarely of two distinct lengths, the shorter less than 0.25 mm long, regularly interspersed with others 0.5-1.0 mm long. Leaves of first monopodial stem usually numerous,

(6-)10-21, spirally arranged, the first leaves scalelike and often soon deciduous, subsequent leaves expanded, membranaceous to chartaceous, divided into an expanded lamina and attenuate base, the attenuate portion plus petiole accounting for 1/8- $\frac{1}{3}(-\frac{1}{2})$ of total leaf length; lamina narrowly to broadly ovate to elliptic or obovate, the margin undulate, the tip acute to acuminate, the base obtuse to cuneate and attenuate into petiole; leaf size increasing with stem height, the largest leaves at middle to upper one-third of stem, then decreasing slightly to stem apex (rarely the largest at apex); total monopodial leaf length 1.5-15 cm, width 0.5-6 cm, the petiole poorly defined, 1-28 mm long. Sympodial leaves membranaceous to chartaceous, the sympodial units difoliate, usually geminate, sometimes appearing unifoliate if subtending dichasial forks, or trifoliate due to bud expansion; largest leaves (often produced by the first sympodial units) similar in shape to those of the monopodial stem, the lamina ovate to elliptic, the margin undulate, the tip acute to acuminate, cuneate at base and short-attenuate into the petiole, becoming reduced, narrower (lanceolate), and subsessile distally; geminate leaves similar in shape, unequal in size, the smaller \(\frac{1}{4} - \frac{3}{4} \) the size of the larger, with a more oblique leaf base; largest leaves 2.5-10.0 cm long, 1.5-4.6 cm wide, the petiole poorly defined, 0.5-10.0 mm long. Leaf pubescence similar throughout, the leaves puberulent, the adaxial trichomes appressed, uniformly pointing at the same angle toward leaf margin, abaxially with trichomes spreading, concentrated on leaf veins, the margins ciliate, the trichomes in all parts of similar length, 0.25-1.0 mm. Inflorescences oneflowered, terminating the stem-units, appearing to be opposite the geminate leaf-pairs or the single leaves of dichasial forks. Pedicels at anthesis green, sometimes with a few purple spots, glabrous to nearly villous, the trichomes spreading to slightly retrorse, straight to slightly undulate, even, 0.5-1.5 mm long; youngest buds (less than 5 mm long) subtended by short, erect pedicels, these elongating, becoming recurved, then erect, 1.9-8.6 cm long when corollas open, usually shorter than the subtending leaves, curved only at tips, the flowers oriented plagiotropically. Calyx at anthesis green, campanulate, 3.0-6.0 mm long, 3.25-6.0 mm wide, truncate, the margin with a hyaline membrane, ten-ribbed, the ribs giving rise to 10 stout teeth at two distinct levels ca. 0.5-1 mm below margin, the teeth variable in shape and length, from small knobs to linear-lanceolate and 7.25 mm long, erect to slightly reflexed, the ribs and teeth glabrous to villous, the trichomes spreading to somewhat retrorse. Corolla sympetalous, slightly nodding; tube short, 1.5-2.5 mm long,

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included in the calyx; limb rotate, 2.0-4.7 cm diam., with five valvate lobes connected nearly to their apices by the corolla membrane; lobes lanceolate to oblanceolate, white with 3-5 violet veins near throat on the adaxial sides, abaxial sides green, curving backwards upon opening, the upper narrower, 2.5-4.5 mm wide, the lower 3-6 mm wide, the tips curved inward in bud and remaining so as the corolla expands; membrane white, translucent, notched at the margin, pulled smooth and taut when lobes open; corolla glabrous except for tips of lobes, these tufted with short trichomes, 0.1 mm long, the membrane near the lobes sometimes short-ciliate. Androecium of five stamens, the filaments of three different lengths, the lowest stamen the longest, the two lateral of intermediate length, and the two upper the shortest; filaments pale green, compressed laterally, sometimes slightly pubescent, elongating each day the corolla opens, the filament of the lowest stamen 2.5-6.25 mm long, elongating more than the others (the lateral 2.0-4.0 mm long, the upper 1.0-4.0mm long), always less than twice the lateral filaments; anthers light yellow, exuding a sweet fragrance, broadly lanceolate to elliptic, the lowest anther 3.25-5.5 mm long, the lateral 3.25-5.25 mm long, upper 3.5-5.5 mm long, the pores of all anthers round to oval, terminal. Gynoecium of two united carpels, the ovules 30-70; ovary conic, 2.5-4.0 mm long, often attenuate into a straight to gently curved style, 7-11 mm long, the stigma captitate, rarely somewhat lobed, slightly oblique, 0.5 mm diam. Fruit a berry without sclerotic granules, light green with lighter or darker green spots or lines when immature, at maturity dull light purple to black, not falling easily from the calyx, turbinate, elongate, 19-75 mm long, 8-19 mm wide, the tip attenuate; fruiting calyx thicker and wider than at anthesis, 2.0-10.0 mm long, 5.0-14.5 mm wide, the teeth stout, stiff, often breaking, drying as fruit matures, remaining appressed to fruit or somewhat spreading, 1-7.5 mm long; fruiting pedicel deflexed, pendent, 3.0-10.0 cm long, swollen at the attachment to the calyx, this swelling 2.5-7.5 mm wide; seeds 3-38, rusty brown to black, reniform to suborbicular, 3.5-5 mm long, 3-4 mm wide.

Distribution. On forested slopes near drainages in the transvolcanic belt of Mexico, states of México, Morelos, and Michoacán, 1,794–2,645 m.

Lycianthes rzedowskii flowers from late July to September and produces fruit from November to January. Specimens of this species have been referred to several other species of Lycianthes such as L. moziniana (Dunal) Bitter, L. somniculenta (Kunze ex Schlechtendal) Bitter, and L. pilifera

(Bentham) Bitter. Lycianthes rzedowskii can be distinguished from other species of series Meizonodontae by its well-developed erect to reclinate monopodial stems with numerous monopodial stem leaves (many of these expanded, rather than scalelike). At the time of flowering, this species has very limited sympodial growth (usually much shorter overall than the main monopodial stem), although in some populations the sympodia elongate during fruit maturation. This species is also distinguished by its combination of smooth white corolla, broad sweetly scented anthers, terminal round anther pores, elongate purple to black fruit, and large brown to black seeds. This species resembles L. ciliolata (Martens & Galeotti) Bitter, a species of limestone soils in the Sierra Madre Oriental that has lilac flowers, and L. acapulcensis (Baillon) D'Arcy, a species with white flowers and a lemony fragrance whose distribution overlaps with that of L. rzedowskii. The best way to distinguish L. rzedowskii from the other two species is to look at the relative lengths of the stamen filaments. In L. rzedowskii the length of the lowest (and longest) filament is never more than twice that of the lateral filaments, while in the other two species, the length of the longest filament is almost always more than twice that of the lateral filaments.

This species is named for Jerzy Rzedowski, who, along with his many students and collaborators, collected many of the Mexican specimens of series *Meizonodontae* that I have studied. I am grateful for his early encouragement of my work and for his help when I visited Mexico.

Paratypes. MEXICO. Morelos: Sierra de Morelos, Cuernavaca, 2,050 m, 26 July 1969, Hinton et al. 17221 (NY); hacia el Valle del Tepeite, Canal Zempoala, Aug. 1932, E. Lyonnet 1002 (CAS, MEXU). México: La Ciénega, 5 km al S de Sultepec, sobre el camino a Amatepec, 2,400 m, 15 jul. 1973, J. Rzedowski 30884 (CAS, ENCB, F); Mpio. Sultepec, NE of Capula along the road to Sultepec, ca. 2.5 rd. km from the outskirts of Capula, 1.0 rd. km NW of the turnoff to Tejupilco, 2,317 m, 13 July 1990, E. Dean & T. Starbuck 212 (BM, ENCB, MEXU, MO, NY, UC, XAL); Mex. hwy. 130, 10.1 mi. N of Temascaltepec, 1,940 m, 27 July 1972, M. Denton 1900 (UC); District Temascaltepec, Comunidad, 2,610 m, 7 July 1932, Hinton et al. 971 (BM, F, G, MEXU); District Temascaltepec, Nanchititla, 26 July 1935, Hinton et al. 8102 (F, GH, MO, NY); Nanchititla, 29 Aug. 1935, Hinton et al. 8234 (GH, K); Nanchititla, Barranca de la Cueva de Santos, downstream from dam, 1,794 m, 9 Nov. 1991, E. Dean et al. 317 (UC, XAL). Michoacán: Mpio. Zitácuaro, near Macho de Agua, E of Zitácuaro, along old hwy. 15, ca. 6-8 rd. mi. E of RR crossing, 2,584-2,645 m, 11 Nov. 1991, E. Dean & T. Starbuck 320 (UC, XAL); Zitácuaro, Cerro Pelón, 17 June 1938, Hinton et al. 11967 (GH, K); along route 15 between K268 and 269, ca. 45 km E of Morelia, 2,830 m, 10 Aug. 1966, R. Cruden 1171 (MEXU, UC); Las Peras, 38 km E of Morelia (ca. 33

km air dist.), km 272 on hwy. 15 (Ciudad Hidalgo to Morelia), 2,515 m, 13 Sep. 1962, R. Ugent & C. Flores 2012 (WIS); Mpio. Queréndaro, along old hwy. 15 ca. 0.4 rd. km W of San José de la Cumbre, near the km 195 marker, 2,500 m, 25 July 1990, E. Dean & T. Starbuck 221 (MEXU, UC); 23 km E of Morelia, km 290 from Mexico City (on old Highway 15), 2,600 m, 28 June 1964, G. Mick & K. Roe 163, 163a (WIS); Mpio. Charo, waterfall along old hwy. 15, E of Morelia, just E of intersection with rd. to Tzitzio, 2,250 m, 13 Nov. 1991, E. Dean & T. Starbuck 322b (UC, XAL), 7 Dec. 1991, E. Dean & T. Starbuck 336 (MO, UC, XAL); Mpio. Charo, along hwy. 15, 20 rd. km E of Morelia, just E of Pontezuelas, 2,165 m, 24 July 1990, E. Dean & T. Starbuck 220 (MEXU, MO, UC); Pontezuelas, 20 km al E de Morelia, sobre la carretera a Zitácuaro (km 289), 2,100 m, 21 jul. 1964, J. Rzedowski 18374 (ENCB, WIS); 13 mi. E of Morelia, 13 Aug. 1947, F. Barkley et al. 2786 (F, TEX).

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